CYTOGENETIC INVESTIGATIONS OF THE FATUOID COMPLEX AND RELATED FACTORS IN AVENA

Sidney Harold Pawlowski

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CYTOGENETIC INVESTIGATIONS OF THE FATUOID COMPLEX AND RELATED FACTORS IN AVENA

A DISSERTATION
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF SCIENCE

FACULTY OF AGRICULTURE
DEPARTMENT OF PLANT SCIENCE

By

Sidney Harold Pawlowski

EDMONTON, ALBERTA

APRIL, 1959

UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES

The undersigned hereby certify that they have read and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Cytogenetic investigations of the fatuoid complex and related factors in _Avena_", submitted by Sidney Harold Pawlowski, B. Sc., in partial fulfilment of the requirements for the degree of Master of Science.

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ABSTRACT

Interspecific crosses between the tetraploid *Avena barbata* (wild type articulation) and the hexaploid species *Avena sativa* (sativa type articulation) indicated dominance of the articulation type of the hexaploid parent. Utilizing lines of the two above species that were monosomic for the c-chromosome in reciprocal crosses resulted in 33- and 34-chromosome F_1 plants. F_1 plants in which the c-chromosome of the sativa parent was missing, developed the fatuoid complex as also did F_1 plants deficient for the c-chromosome from both parents.

The nullisomics obtained in several different hexaploid species all showed the wild type articulation and other factors of the fatuoid complex. Plants that were nullisomic for the c-chromosome pair were highly sterile due to very marked disturbances during meiosis. The degree of pubescence of lemmas in the tetraploid and hexaploid species was found to be proportional to the number of the c-chromosomes present carrying the factor for pubescence. Absence of both c-chromosome resulted in glabrous lemmas. Reciprocal crosses involving *A. fatua* and monosomic sativa indicated that delayed germination was recessive to the germinative capacity of the sativa parent. Definite evidence was obtained that the genetic make-up of both the embryo and surrounding maternal tissue are factors in delaying germination. Since monosomic F_1 seed resulting from monosomic Aurora x *A. fatua* cross germinated as readily as the disomic F_1, no evidence was obtained to indicate a possible linkage of the fatuoid complex with a factor for dormancy.

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CYTOGENETIC INVESTIGATIONS OF THE FATUOID COMPLEX AND RELATED FACTORS IN AVENA

INTRODUCTION

Fatuoids, sometimes referred to as "false wild oats" have been found in most varieties of cultivated oats. They resemble *Avena fatua* in that each grain of the spikelet has a twisted geniculate awn, a pubescent rachilla and an oval disarticulation base surrounded by dense pubescence. This group of diagnostic characters is referred to as the fatuoid complex. In other respects fatuoids are similar to the particular variety in which they occur. Fatuoids, if fertile, will breed true for the fatuoid complex and are therefore referred to as homozygous fatuoids.

Heterozygous fatuoids are more or less intermediate between the normal and fatuoid in most characteristics. The heterozygous fatuoids have a twisted geniculate awn only on the primary kernel of each spikelet. Secondary and tertiary grains of the spikelet are awnless and indistinguishable from the normal variety. The base of the primary kernel shows a slight pubescence, nevertheless it resembles *Avena sativa* more than *Avena fatua*.

It is generally agreed that homozygous fatuoids arise from heterozygous fatuoids, however, the origin of heterozygous fatuoids

has been a controversial issue for a number of years with certain aspects of this problem still not generally agreed upon.

The work reported in this thesis deals with cytological studies of heterozygous fatuoids and their progenies. Interspecific crosses using lines monosomic for the c-chromosomes in both the 42- and 28-chromosome species of Avena were used to compare the inheritance of the fatuoid complex and other characters that may be associated with these chromosomes. Certain aspects of dormancy in Avena fatua were also given special study.

REVIEW OF LITERATURE

Genetic Studies

Most heterozygous fatuoids studies prior to 1925 were found to segregate normals, heterozygous fatuoids and fatuoids in a ratio approaching 1:2:1. Further studies indicated the presence of strains whose segregation ratios varied considerably.

Goulden (8) selected heterozygous fatuoids from a threshed sample of Beaver. While most plants were found to segregate in a ratio approaching 1:2:1, one segregated 20 normals, 15 heterozygous fatuoids and 5 fatuoids, of which two were dwarf. Another heterozygous fatuoid gave no normals, 12 heterozygous fatuoids and 18 sterile fatuoids. These two segregation types were later classed as C and "modified B series" respectively by Huskins (14).

Nishiyama found a heterozygous fatuoid in a plot of Victory oats which gave 7 normal, 6 heterozygous fatuoids and 1 sterile dwarf fatuoid. In later generations involving thousands of plants, heterozygous fatuoids of this strain gave the three types of progeny in a 1:30:1 ratio. This strain was classed as Series B.

Huskins (14) classed these fatuoids into series A, B. C and modified B on the basis of their segregation ratios. The segregation ratios of normals: heterozygous fatuoids: fatuoids of series A, B, C and modified B are 1:2:1, 1:5:few, 1:1:few and 1:5:numerous respectively. Fatuoids belonging to the A series are the most common. Fatuoids belonging to other series are usually discovered following more intensive investigation.

Goulden (8) found that in the dwarf fatuoids the pollen mother cell meiosis was grossly abnormal. He suggested that at least part of a chromosome which also carries the gene or genes for the sativa type articulation was missing.

Huskins, (13), in studying the origin of speltoids which appear to have the same genetic basis as fatuoids, discovered the origin of the B and C strains of speltoids. He found that B series were monosomic and lacked a c-chromosome. The C series was the result of segregation from a heteromorphic bivalent rather than the presence of an extra chromosome as he and other workers had perviously presumed. Shortly after, Nishiyama and Uchikawa, working independently, found an identical situation in a strain of fatuoids.

The chromosome numbers of heterozygous plants of series A, B, C, and modified B are 42, 41, 40 plus a heteromorphic pair and 41 respectively. In the modified B series the heterozygotes produce normals and heterozygous fatuoids in the usual B series, but also produce numerous instead of few fatuoid offspring. Most of the fatuoids are dwarf and sterile as in the typical B series. Evidently the mutant pollen produced by the heterozygous fatuoids of the modified B series functions as well or better than their normal pollen. However, the homozygous mutant besides being dwarfed produces abortive pollen and is almost completely sterile. The diverse segregation ratios that may be obtained from phenotypically similar mutants depend upon the particular aberrant constitution of the mutant, the frequency with which different types of gametes are formed and the differential functioning of aberrant ovules and pollen in fertilization.

Cytological examination of the pollen mother cells of nullisomic homozygous fatuoids by Huskins (11) Goulden (8) and Nishiyama (23) revealed extremely irregular meiotic divisions. In most cells no regular metaphase plates were found and the bivalents observed were loose end-to-end associations. Nishiyama (23) observed a maximum of ten open bivalents in pollen mother cells. Such an effect on chromosome pairing is not found in any of the nullisomic lines of wheat obtained by Sears (29). He obtained only one nullisomic (null. III) that rendered plants partially asynaptic, but this did not depress their fertility. Ramage and Suneson (4) obtained a nullisomic in Avena byzantina which is relatively stable through meiotic divisions and has sufficient fertility to be usable in breeding programs.

Huskins and Sander (13) are of the opinion that all heterozygous fatuoids arise through a chromosome aberration similar to the case of the three segregation-types of speltoids. The speltoids arise as a result of deficiencies which range from a whole chromosome designated as number 9 by Seare (28) down to a segment of chromosome 9 which is too small to be established microscopically with certainty at metaphase but still determinable genetically as a deficiency and not a single gene mutation. In the oat mutants there are similar deficiencies but the range apparently extends below the present limit of both cytological and genetic determination. It cannot yet definitely be differentiated from gene mutation though no evidence favors the latter alternative. Nishiyama and Uchikawa agree with Huskins that the B and C series are the result of whole chromosome loss and a segmental deficiency respectively but are of the opinion that strain A originates as a result of a gene mutation.

Use of Monosomics and Nullisomics in Genetic Studies

Sears (29) and Unrau (31) used monosomics and nullisomics in cytogenetic studies of common wheat. Monosomics are plants deficient for an entire chromosome and have now been obtained in several polyploid species. Nullisomics are plants that are deficient for a pair of chromosomes. These are not obtained as readily as monosomics because the chromosome deficiency is usually transmitted with a fairly high frequency through the eggs but only rarely through the pollen. The frequency of occurrence of the nullisomic associated with the fatuoid character reported by Huskins (12) is an exception in that the deficiency is transmitted with a high frequency through both the egg and pollen.

Nishiyama (21) studied spikelet type in oats utilizing a line of oats that was monosomic for the c chromosome pair associated with

the fatuoid character. He crossed Avena fatua, Avena sterilis and Avena nuda with a 41 chromosome (B strain) heterozygous fatuoid from Avena sativa var. Aurora. The nullisomics (2n-2c) progenies from the Avena fatua and Avena sterilis x monosomic sativa cross had fatuoid spikelets. The monosomics resulting from the A. nuda cross had either naked or solid spikelets whereas the nullisomic progeny had either fatuoid or naked spikelets.

It was also noted that chromosome c in Avena fatua affects the development of hairs on the lemma of the first grain and to a lesser extent on the lemma of the second grain.

Interspecific Crosses

Inter-diploid species crosses between Avena wiestii (wild type articulation) and Avena brevis (sativa type articulation) exhibited dominance of the wild type articulation (17).

The F_2 generations segregated into four grain base types. Two were of the expected parental type and two were new types not observed in the hexaploid group. Jones designated these two new types as X and Y.

The X type is distinguished by the occurrence of a pedicel which remains adherent to the base of the lower grain of the spikelet and the free end of the pedicel carries with it a small bulk of callus. The rachilla is hairy and on separation of the lower and upper grains it generally remains attached to the upper grain in a manner characteristic of the species A. sterilis.

The lower grain in the Y type shows a restricted articulating surface resembling that of the wild type, but with the articulation surfaces less well defined. The articulating surface of the upper grain is much reduced and approximate to that found in the upper grains of plants possessing the normal type base.

In the F_2, the wild, X, Y and normal types occurred in a 9:3:3:1 ratio respectively. The cross between X and Y type gives rise to F_1 plants possessing seed with fully developed wild type bases indicating that the wild type is determined by the interaction of the two main factors, X and Y.

In the tetraploid group crosses made between A. abyssinica (normal base) and A. barbata (wild base) indicated dominance of the wild type base.

Segregation in F_2 gave four phenotypic classes agreeing closely, morphologically with those found in the diploid. The numbers present in each class may be explained on the basis of a four-factor difference between wild and normal type parents. The X and Y genes show independent segregation and the simplex condition of the X and Y genes shows dominance over the triplex recessive condition for normal type base.

In a triploid resulting from the cross Avena longiglumis (diploid wild base) and Avena abyssinica (tetraploid normal base), the wild base proved dominant. When the same diploid parent was crossed with A. sativa (hexaploid with normal base) the tetraploid F_1's gave grain with almost completely normal type base. Pentaploid F_1 plants derived from crossing A. barbata (tetraploid wild base) with A. sativa produced a type of base approximately like that of the hexaploid parent.

Crosses between weak and strong awn species along with different base types in the diploids did not indicate linkage between base type and awn type.

The genes inhibiting awn development appear to be closely linked with the gene or genes which inhibits the development of the wild type base. Series A. fatuoids appear to be due to a small deficiency in or deletion of the loci carrying the linked inhibiting genes (17).

Studies of Dormancy

Coffman and Stanton (4) compared the germinative ability between fatuoid and normal oats of the same variety grown in the field and also under greenhouse conditions. When dormancy occurred in the normal plants of a variety of oats, it also occurred in the fatuoids from that variety, and when germination was prompt, the seed of either the homozygous or the heterozygous forms also germinated promptly.

In studying the inheritance of delayed germination in hygrids of *Avena sativa* and *Avena fatua* Johnson (16) found that germinability is genetically dominant over non-germinability (delayed germination). He also found that germinability is inherited on the basis of three factors of more or less equal potency, one of which is linked with the factor for grain type. The correlation between high degree of germinability and sativa type of grain was very marked. There also appeared to be a tendency for fatua type to be less germinable than the intermediate types. There were indications that at least one of the non-linked factors has less potent capacities than the linked factor and thus was capable of producing germinability only after a longer period of after-ripening than was required by the linked factor. It is inferred that very shortly after harvesting only embryos with six dominant allelomorphs are germinable and as time goes on embryos with a progressively smaller number of dominant allelomorphs become germinable.

Johnson (15) found that F_2 plants of the *A. sativa* x *A. fatua* cross grown at different locations produced seeds that required different periods of time of after-ripening before the seeds would germinate.

This indicates that growing conditions can be a factor in causing a difference in degree of dormancy.

In studying the physiology of delayed germination in Avena fatua, Johnson (15) found variations in the after-ripening periods required by a number of different selections. Evidence was obtained which strongly indicated that delayed germination is determined by a condition of the seed coat which develops after fertilization. Hay (10) found that when incompletely after-ripened grains were subjected to a germination test, secondary dormancy was induced. However, dormancy could be more or less completely overcome by breaking the seed coat over the embryo or by soaking the seeds in a solution of potassium nitrate. An increase in the oxygen-concentration of the atmosphere has long been noticed to stimulate germination (15). The reasons for stimulation of germination in the case of breaking of the seed coat is presumed to be due to more rapid penetration of oxygen to the embryo. The stimulation by potassium nitrate might be considered as resulting from: (a) direct germinative stimulation by the absorbed anion; (b) indirect effects of the absorbed anions such as increased utilization of stored carbohydrates or the acceleration of organic acid formation following reduction; and (c) chemical effects upon the seed coat which increase permeability to oxygen (15).

Soaking of non-dormant seed of Avena fatua in boiled water at 25°C. for 12 hours will also induce dormancy (10). The seed will germinate if the hulls are removed at that time but if not removed until after four days on filter paper the seed, although still viable, will not germinate.

Naylor and Christie (22) studied the effect of ground hull

of Avena fatua on the development of dormancy in dehulled caryopses under nitrogen (no oxygen). Seed and ground hull were separated by a sheet of filter paper. A significantly greater degree of dormancy (62%:16%) was induced in the treatment which included hull. Since the ground hull was separated from the seed by filter paper, it appears that a water soluble or volatile substance originating in the hull exerts the observed effect on dormancy.

It was noticed that the respiratory quotient of the seeds (initially close to unity) began to fall after the second day of induction treatment. During this time dormancy was beginning to increase. After the sixth day the R.Q. had declined to 0.69 which could indicate a change in respiratory substrate from carbohydrates to fats during the onset of dormancy. Such a change might occur if the germination inhibitor specifically prevented the utilization of carbohydrate reserves in the endosperm. This is a possibility since Elliott and Leopold (6) report detecting a germinator inhibitor in Avena sativa which inhibits the activity of alpha and beta amylase.

The dormancy of the upper seed of Xanthium is generally quoted as a classical example of dormancy due to the relative impermeability of the testa to oxygen (7). However, Wareing and Fonda (32) report that certain germination inhibitors in the embryo as well as oxygen effects are involved. This inhibitor is readily extracted in water but is not heat stable as is the one reported in Avena sativa (6). An enzyme preparation from the embryos was obtained which was capable of destroying the inhibitor in vitro in the presence of oxygen. These observations suggest that the inhibitor may undergo enzymically controlled breakdown in the presence of oxygen. This would indicate that the stimulation of germination by increased oxygen

tension is due to a specific effect upon the breakdown of the inhibitor rather than to an increase in the rate of respiration and general metabolism.

Generally roots are much more sensitive to the inhibitor than the coleoptile, plumule or young sprouts (7).

MATERIALS AND METHODS

Heterozygous fatuoids used in this study were found in foundation stock of Victory oats being maintained at the University of Alberta. These were grown in the field and analysed cytologically. Several fatuoid selections were crossed with normal Victory and their segregation ratios were checked.

The following material was supplied by Ichizo Nishiyama. A heterozygous fatuoid with 41 chromosomes ($20\ \underline{II}$ + c-chromosome) from the variety Aurora which segregates normals, heterozygous monosomic fatuoids and fatuoids in a ratio of 1:15:10, and a monosomic steriloid which was found in the progeny of *Avena barbata* ($n=14$) x *Avena strigosa* ($n=7$) with a chromosome number of 27 ($13\ \underline{II}\ 1^{\underline{I}}$). This plant generally segregates two kinds of progeny with $2n=28$ (wild type articulation of grains) and $2n=27$ chromosome with steriloid type of articulation of grains. The primary kernels and secondary kernels of both the 27- and 28-chromosome plants are awned and have densely pubescent base and rachilla. The lemmas of both primary and secondary kernels

on the 28-chromosome plants are densely pubescent (figure 1) but on the 27-chromosome plants, only the primary kernels have a slightly pubescent lemma. (figure 2).

Since these will be the only 27- and 28-chromosome plants used, they will be referred to by their respective chromosome numbers in this report.

Reciprocal crosses were made between the monosomic Aurora and the 28-chromosome plant.

Rodney was crossed with the Aurora monosomic to check the effect of the monosomic condition in the hybrid from the standpoint of morphological appearance and segregation ratios.

The Aurora monosomic was crossed with Avena fatua to study the potency of the dormancy factor linked with the grain type factor.

It was planned to make counts of the number of bivalents formed in the pollen mother cells of the nullisomics appearing in the progenies of the above two crosses as compared to the nullisomics arising in Aurora.

F_2 seed from a cross between MC44 and a giant off-type occurring in Ajax was supplied by F. J. Zillinsky. There were frequent micronuclei observed in the tetrad stages of this material and it was hoped that some nullisomics could be obtained in its progeny.

Several plants resembling heterozygous fatucids were observed in some Kanoto oats from seed received from F. J. Zillinsky. Cytological analysis proved one plant to be monosomic.

It was not known whether the missing chromosome was a c chromosome, thus resulting in heterozygous fatuoids. Several florets

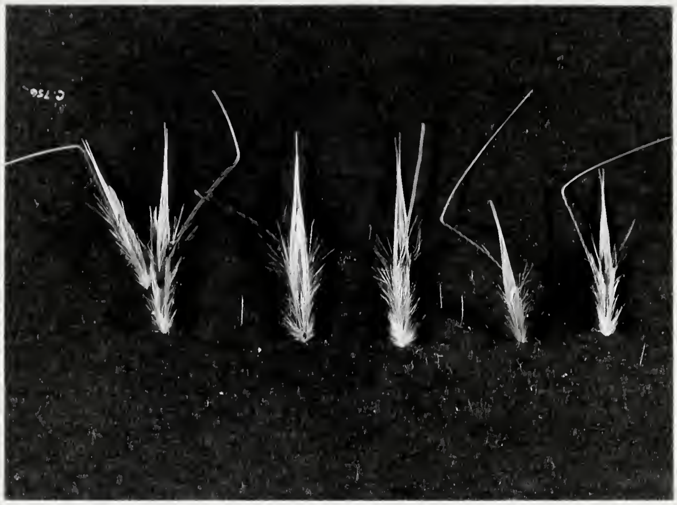

Figure 1. Floret of the 28-chromosome plant showing wild type articulation and pubescence of kernels.

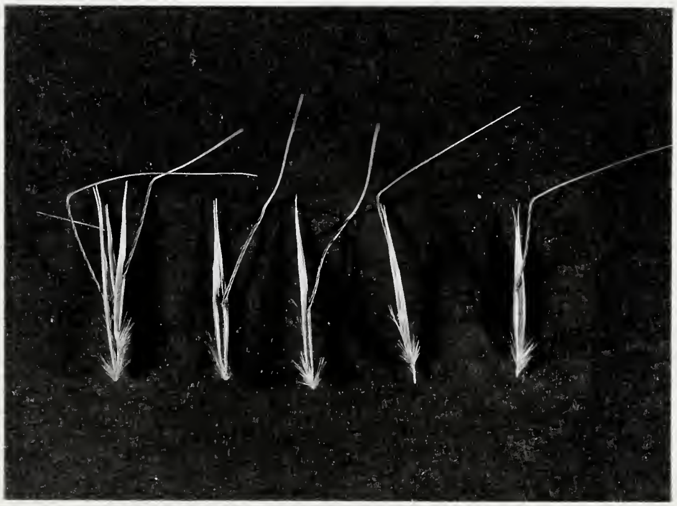

Figure 2. Floret of 27-chromosome plant showing steriloid type articulation and slight pubescence on the lemma of the primary kernel only.

of the Kanota monosomic were pollinated with pollen from Avena fatua to check whether the deficiency was a c-chromosome. Since this plant was from a late seeding, reciprocal crosses were made with the 27-chromosome plant which was the only plant available.

Reciprocal crosses between normal disomic Kanota and the 27-chromosome plant were also attempted.

Seeds were germinated on moist filter paper in covered petri dishes prior to planting in the greenhouse. Seeds that appeared to be dormant were induced to germinate by removing the hull, scratching the seed coat covering the embryo, drying and wetting alternately, or cutting off a portion of the caryopsis. Embryo culture was used to grow seeds that failed to germinate after other methods were tried.

The hulls and the pubescent covering of the soaked seeds were removed. This prevents any air locks and thereby insures better sterilization of the seed. The seed was then sterilized by immersing it in a mercuric chloride solution (conc.1/1000) for two minutes and rinsing in sterile distilled water. The seed coat of dormant seeds that has been soaked for several days becomes loose and very pliable and is easily removed with a pair of forceps to expose the embryo. The embryo was removed with a sterile wire loop and placed directly on to Orchid Agar kept free from contamination in covered test tubes or special vials. If an embryo became contaminated in the process of removal, it was immersed in mercuric solution for half a minute and rinsed in sterile distilled water before placing it on the culture medium.

After plants had grown to a height of 2-3 inches, they were removed from the culture medium and planted into soil in the greenhouse.

In order to test whether the dormancy was due to some factor present in the oat hulls, the hulls were saved from the kernels which failed to germinate but proved viable when cultured on orchid agar. The caryopses of mature Ajax oats were placed into these hulls to see what effect they would have on normal germinable kernels. Mature Ajax oats with the hulls removed and then replaced were used as a check. Some of these hulls were ground and applied to the naked caryopses of Ajax oats. Hulls from Ajax oats were ground and used as a check. Seeds were germinated on moist filter paper in covered petri dishes.

Some of the hulls from dormant seeds were placed in a small vial and covered with a small quantity of distilled water. This was kept covered at room temperature for 48 hours. Then the water extract was filtered off. Dry embryos of normal Ajax oats were pared off together with some endosperm and soaked in this water extract for 10 hours. The embryos were removed and sterilized in mercuric chloride (conc. 1/1000) for $\frac{1}{2}$ a minute. Adhering endosperms and seed coats were carefully removed and the embryos were placed on different culture media. A check treatment was done following the same method using normal Ajax oat hulls.

Three types of culture media were used. Orchid Agar was one and the other two were made up in the following manner.

White's stock mineral.

$MgSO_4$	3.6 gms.	) dissolved in 500 ml. distilled
Na_2SO_4	2.0 "	) water.

$Ca(NO_3)_2.4H_2O$	2.6 gms.	dissolved in 500 ml. distilled water.
KNO_3	800 mgs.	
KCL	650 mgs.	
$NaH_2PO_4.H_2O$	1.65gms.	

The two solutions were mixed together.

Trace elements:Nitsch's - 1 liter

Conc. H_2SO_4	1.5 ml.
Mn $SO_4.4H_2O$	3.0 gms.
Zn $SO_4.7H_2O$	500 mgs.
H_3BO_3	500 mgs.
$CuSO_4.5H_2O$	25 mgs.
$Na_2MoO_4.2H_2O$	25 mgs.
Co $Cl_2.6H_2O$	46 mgs.
Dist. H_2O	1000 ml.

Iron solution - 0.25 gms. powdered ferric citrate dissolved in 100 ml. boiling water.

Final Mixture:

White's stock mineral	100 ml.
Nitsch's trace element	1 ml.
Iron solution	4 ml.
Distilled water	890 ml.

This final mixture was divided into two lots and approximately 20 gms. of wheat starch was added to one. Then a sufficient amount of Bacto-Agar was added to both to form a gel of the same consistency as that of the Orchid Agar. The media were heated to dissolve the Bacto-Agar and then poured into vials used for growing the embryos.

The media were autoclaved at 15 pounds live steam for 20 minutes.

RESULTS AND DISCUSSION

Cytological observations of the P.M.C. (pollen mother cells) of heterozygous fatuoids in Victory proved most of the plants to have 42 chromosomes which paired normally. Several fatuoid plants produced occasional micronuclei as a result of lagging chromosomes at metaphase, while in one plant two chromosomes were observed that failed to pair occasionally. The fatuoids showing abnormalities were crossed with normal Victory and their segregation ratios of normals, heterozygous fatuoid and fatuoids was found to fit the 1:2:1 ratio.

This indicates that the fatuoids obtained from foundation stock of Victory variety belong to the A series which is the most common type. The meiotic irregularities observed were not related to the fatuoid complex. Apparently, meiotic irregularities are fairly common in oats. (2, 19). There is a possibility that the heterozygous fatuoids used in this study may have originated from very few plants, thus limiting the possibility of obtaining fatuoids belonging to different series.

Reciprocal crosses between the Aurora monosomic (sativa base) and the 28-chromosome species (wild base) were successful only when the 28-chromosome plant was used as the female. This was unexpected since generally (20) greater success is obtained when the species with the lower chromosome number is used is the male parent. It may have been the result of poor pollen produced by the 28-chromosome species under those particular conditions. Thirteen plants grown from the

above cross resulted in three 35-chromosome plants, and ten 34-chromosome plants. Articulation in the 34-chromosome plants was of the wild type with dense pubescence on the lemmas of both lower and upper florets, (figure 3). All the florets in a spikelet were awned. The 35-chromosome plants had solid bases and slight pubescence on the lemmas of the primary kernel only, (figure 4). The first tillers produced awnless florets, while later tillers produced awned and awnless florets on the same panicle. When awns were produced, there were present on the primary kernel only. Several months later when the above crosses were repeated, all 35-chromosome F_1 plants produced awns on the lemmas of primary kernels.

The absence of awns on some of the florets may be due to environmental effect as found by Huskins (12). Further evidence of this was shown when the heterozygous fatuoid grown under the same conditions as the 35-chromosome plant produced a similarly weak awn. In the 34-chromosome plants in which the c-chromosome from the sativa species is absent there is a full expression of the fatuoid complex, but in the 35-chromosome plants where the c-chromosome of *A. sativa* is present, the heterozygous fatuoid appearance is expressed. The presence of the c-chromosome from the sativa parent affects the degree of expression of pubescence on the lemmas of the primary and secondary florets.

Cytological observations of over 100 pollen mother cells of 34- and 35-chromosome plants (figures 5 and 6) indicated an average of 6 and 7 open bivalents respectively.

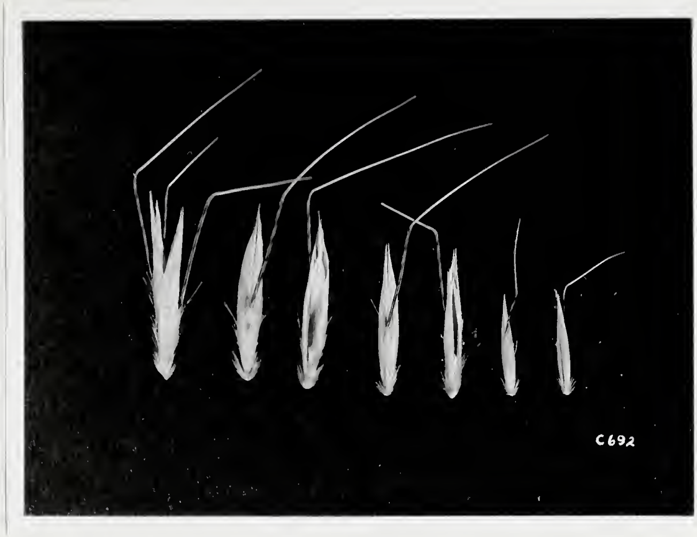

Figure 3. Floret of the F_1 plant where a 20-chromosome gamete of Aurora and a 14-chromosome gamete were effective in fertilization.

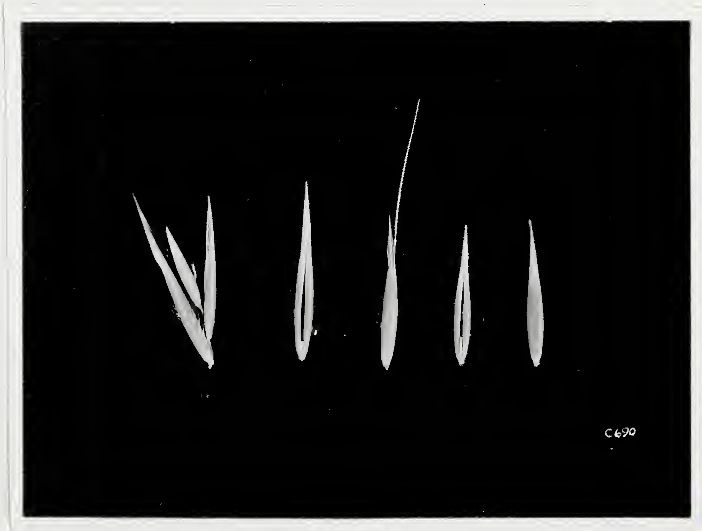

Figure 4. Floret of the F_1 plant where a 21-chromosome gamete of Aurora and a 14-chromosome gamete were effective in fertilization.

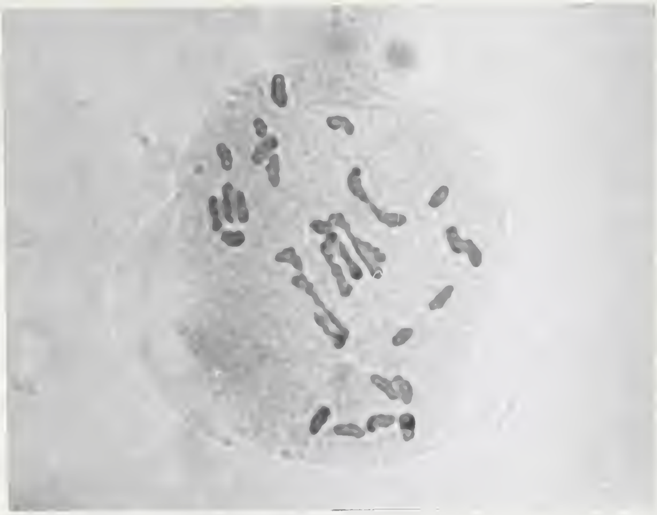

Figure 5. P.M.C. of 34-chromosome F_1 showing 5 open bivalents, one trivalent and 21 univalents.

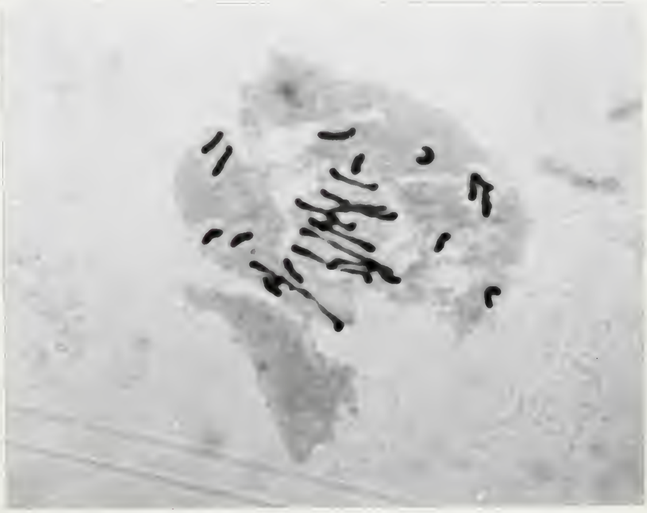

Figure 6. P.M.C. of 35-chromosome F_1 showing 8 open bivalents, one trivalent and 16 univalents.

Only on several occasions a closed bivalent was observed. Further irregularities were observed in chromosome associations in that fairly frequent trivalents were present as seen in figures 5 and 6 and occasional chains of three and four chromosomes. The maximum number of chromosome associations in the 34- and 35-chromosome plants was 8 and 9 open bivalents respectively.

Reciprocal crosses between the Kanota monosomic and the 27-chromosome steriloid supplied by Nishiyama resulted in a few seeds when Kanota was used as the male parent. No seed was obtained from crosses where Kanota was used as the female parent. Four plants were obtained from the cross Kanota monosomic x the 27-chromosome plant. Two plants had florets with sativa type articulation, glabrous lemmas and an awn on the primary kernel only, (figure 7). The awn originated at an unusually high point on the lemma. The chromosome number of these plants was found to be 34. This would indicate that the 21- and 13-chromosome gametes were effective in fertilizations. Floret articulation resembled the tetraploid parent in that the rachilla adhered to the secondary kernel (figure 7). However, this proved to be an environmental effect since the floret articulation of the majority of the later tillers resembled the hexaploid parent.

The spikelets of these plants strongly resembled the 35-chromosome plants of the Aurora monosomic by 28-chromosome cross in all respects except in pubescence of the lemma of the primary kernel. Apparently the gene for pubescence of the lemma is associated with the missing chromosome of the tetraploid parent.

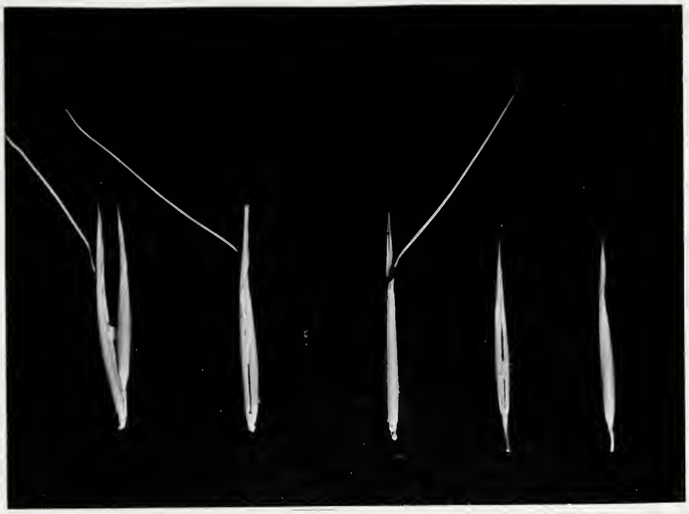

Figure 7. Floret of the F_1 plant where a 21-chromosome gamete of Kanota and a 13-chromosome gamete were effective in fertilization.

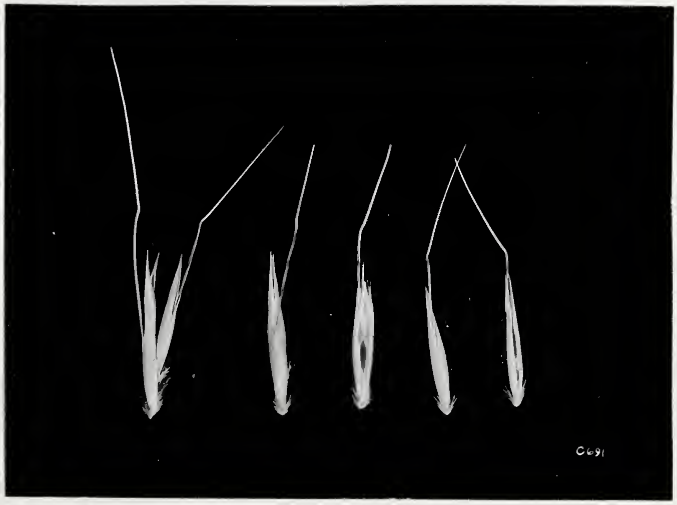

Figure 8. Floret of the F_1 plant where a 20-chromosome gamete of Kanota and a 13-chromosome gamete were effective in fertilization.

Another F_1 plant of the cross Kanota monosomic x the 27-chromosome plant had wild type articulation of florets and the lemmas of both primary and secondary kernels were awned and heavily pubescent. The chromosome number of this plant was found to be 34. Apparently in this instance a 20-chromosome gamete from Kanota and a normal gamete from the tetraploid were effective in fertilization. Spikelets of this plant resembled the 34-chromosome plants resulting from the Aurora monosomic by the 28-chromosome species cross, indicating that the missing chromosome in Kanota is a c-chromosome associated with the fatuoid character.

The fourth plant of this cross (figure 8) had floret articulation of the wild type, glabrous lemmas and awns on the lemmas of all florets. The chromosome number of this plant was found to be 33 (figure 9). This would mean that the 20- and 13-chromosome gametes were effective in fertilization.

This fives further evidence that the missing chromosome in Kanota is the c-chromosome and that the missing chromosome in the 27-chromosome species carries the factor for pubescence of the lemma.

The cross between normal Kanota and the 27-chromosome plant resulted in one plant which had floret articulation of the sativa type and glabrous lemmas with awns on the primary kernel only. The chromosome number was found to be 34 which means it is of the same genetic constitution as the plant in figure 7.

In some of the above crosses involving Kanota, some difficulty was encountered in determining the articulation type before the panicles were well matured. Although disarticulation of some of the florets of wild type F_1 plants was not as easy as those involving Aurora,

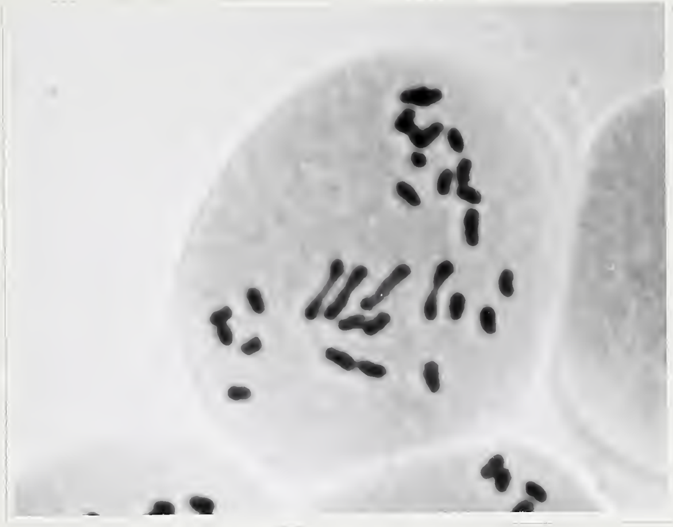

Figure 9. P.M.C. of 33-chromosome F_1 showing 4 open bivalents and 25 univalents.

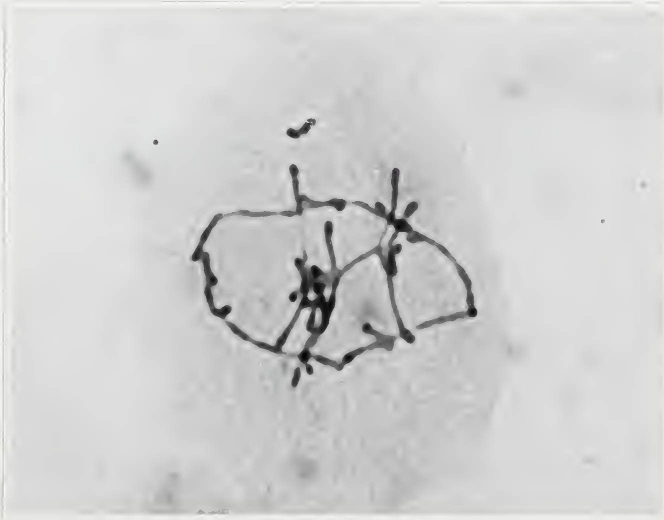

Figure 10. Ring of 12 chromosomes observed in 33-chromosome F_1 plant.

a well developed fatuoid base was present on each kernel. All the F_1 plants were sterile.

Cytological observations of P.M.C.'s of the F_1 of the Kanota monosomic by the 27-chromosome plant revealed an average bivalent formation of 6 open bivalents in the 34-chromosome plants. Trivalents were observed quite frequently as well as an occasional ring of three and chain of 4 chromosomes.

The 33-chromosome plant had 5 and 6 open bivalents in approximately equal frequency. An occasional trivalent was observed. One large chromosome ring was observed (figure 10) which appears to consist of 12 chromosomes. Cytological studies of additional P.M.C.'s did not indicate a possible explanation for the formation of such a large chromosome ring.

One seed was obtained from a 34-chromosome F_1 plant resulting from a 28-chromosome and monosomic Aurora cross. This F_2 plant was found to have a chromosome number of 54. Cytological observations of P.M.C.'s indicated a maximum bivalent formation inclusive of trivalents to be 24. The average bivalent count was 20. Floret articulation was still of the wild type and the pubescence of the lemmas of all kernels of the spikelet was as long and as dense as that of the tetraploid parent. The pubescence of both lower and upper florets indicates that two c-chromosomes from the tetraploid parent are present in this plant. Unfortunately, the plant was sterile.

The 54-chromosome F_2 plant could be the result of the union of 34- and 20-chromosome gametes. Although this would account for the formation of only 20 bivalents, the additional ones may be attributed

to autosyndesis. The union of gametes of other chromosome numbers is also possible. Since the bivalent counts in the F_1 varied from 1 to 8, a combination of this variability and the random movement of univalents to the poles could give rise to gametes with a wide range of different chromosome numbers.

Rodney x Aurora monosomic

Four seeds were obtained from the Rodney x Aurora monosomic cross. Two of these plants were heterozygous fatuoids which upon cytological examination were found to be monosomic. Seeds of these two monosomic plants were grown and produced two normal plants, eight monosomic and 12 nullisomic plants. The nullisomic plants showed the disturbed meiosis with a low number of bivalents (figure 11). All the kernels of the nullisomic plants had the wild type base as well as the other features of the fatuoid complex. They were all completely sterile. One of the plants with morphological characteristics of a heterozygous fatuoid, which would normally be expected to be a fertile monosomic, was found to have 41 chromosomes (figure 12) but was sterile. Meiotic irregularities were similar to those found in the nullisomic fatuoids. Maximum chromosome associations were 10 open bivalents.

It was evident that crossing Rodney and the Aurora monosomic did not affect the number of bivalents formed in the resulting nullisomics as compared to the nullisomics in the original Aurora. Nishiyama found heterozygous fatuoids with a heteromorphic chromosome pair (a c-chromosome plus a long arm of c) to be fertile. Fatuoids that were homozygous for this deficiency were also fertile. The sterility of the heterozygous monosomic fatuoid from the above cross may be due to

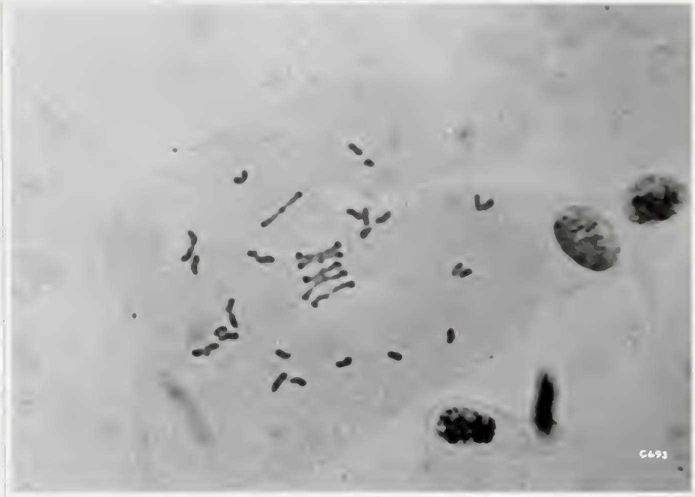

Figure 11. P.M.C. of 40-chromosome Aurora monosomic X Rodney F_2, showing 6 open bivalents and 28 univalents.

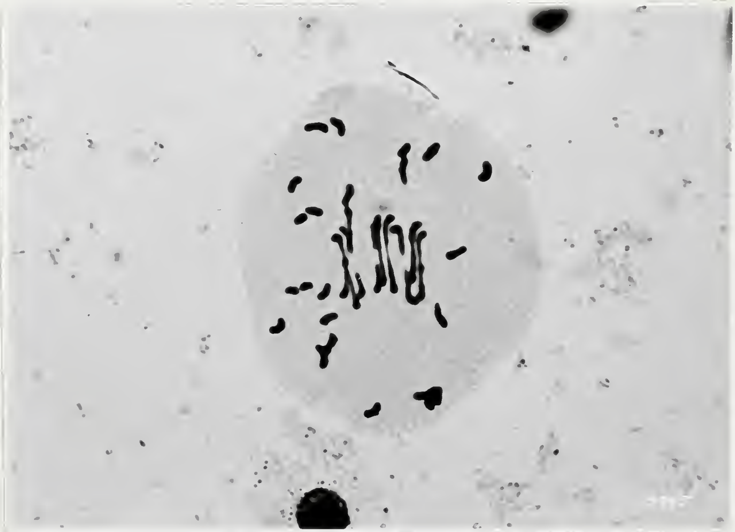

Figure 12. P.M.C. of 41-chromosome Aurora monosomic X Rodney F_2, showing 9 open bivalents and 23 univalents.

a loss of part or all of the arm of the chromosome which apparently carries the gene or genes that brings about normal chromosome pairing. Asynapsis occurs when the c-chromosome pair is absent.

Monosomic Aurora and Monosomic Kanota x *Avena fatua*

Fourteen F_1 plants were obtained from the seed of the Aurora monosomic and *Avena fatua* cross. The kernels of all the F_1 plants were awned and had the fatua base on each kernel of the spikelet (Figure 13). The lemmas of the first kernels were pubescent and the lemmas of the second kernel of the spikelet showed very slight pubescence. Cytological examination indicated that all these plants were monosomic. These results are in agreement with those obtained by Nishiyama (23).

Five plants were obtained from the seed of the Kanota monosomic and *Avena fatua* cross. All portrayed the same characteristics as the F_1 plants resulting from the Aurora monosomic cross. Cytological examination indicated that all these plants were monosomic.

Attempts to germinate the seed produced by the F_1 plants of the above two crosses resulted in approximately 5 per cent germination, whereas, fatuoids in Victory oats grown under the same conditions germinated readily. Treatments like removing the hull, scratching the seed coat, cutting off part of the caryopsis and alternate drying and wetting resulted in an additional 10 per cent germination. The majority of the F_2 plants grown were obtained by removing the embryo from the seed and culturing it on Orchid Agar.

Although no 42-chromosome F_1 hybrids between *A. sativa* and *A. fatua* were obtained to compare the germinability of their seed to that of the monosomic hybrids, it was found that a much higher percentage of the seeds were dormant than reported by Johnson (15).

In the process of alternate drying and wetting of dormant seed, a number of seeds appeared to commence germination but did not progress much further than the most advanced stage illustrated in figure 14. Upon closer examination it was seen that only the coleoptile was developing and the radicle remained dormant. According to Evenari (7) roots are much more sensitive to inhibitors than the coleoptile, plumule or young sprouts, consequently, it appears that the concentration of the inhibitor was great enough to affect the development of the radicle only.

Cytological analysis of the pollen mother cells of the F_2 plants indicated the presence of plants with chromosome numbers ranging from 38 to 42. Plants with this range in chromosome numbers were found in both, the Aurora and Kanota monosomic x Avena fatua progenies. The average number of bivalents observed in plants of the same chromosome number varied considerably. This is probably due to differences in the chromosomal make up of these plants. Chromosome pairing in the 41-and 42-chromosome plants appeared to be normal except for the presence of 2 to 5 univalents in approximately 10 per cent of the P.M.C. The maximum number of bivalents observed in plants with 40 chromosomes or less were 9 open bivalents. Closed bivalents were very rare. Most plants showed no abnormalities in chromosome pairing other than the low number of bivalents formed. In a few plants a trivalent was observed quite frequently and occasionally a chain of 4 chromosomes.

Out of 60 F_2 plants from the Aurora monosomic and Avena fatua cross, only 12 proved fertile. Similarly, only 3 plants out of 38 proved fertile in the F_2 involving the Kanota monosomic and Avena fatua

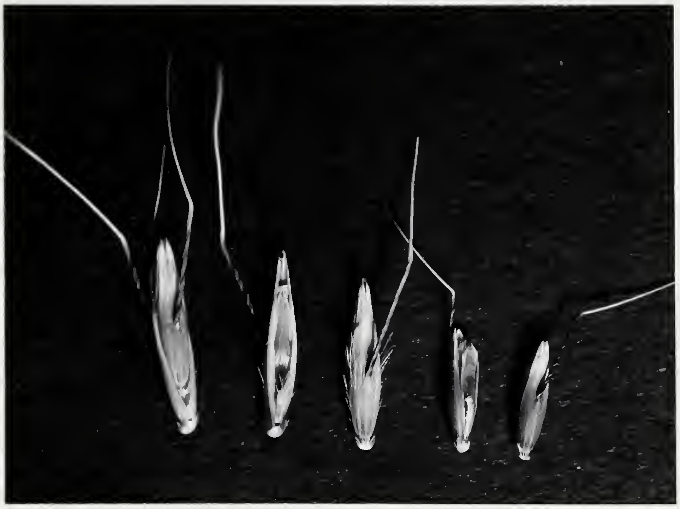

Figure 13. Floret of a monosomic F_1 plant from Aurora monosomic x A. fatua cross.

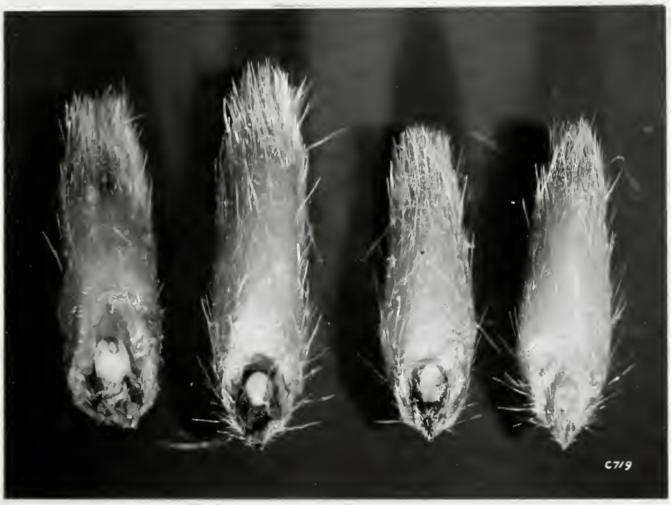

Figure 14. F_2 seed from the above cross showing development of the coleoptile but not the radicle.

cross. Pubescence on the lemmas of all fertile plants indicated that either one or both of the c chromosomes from Avena fatua was present. All the sterile plants had glabrous lemmas.

Eight of the twelve fertile F_2 plants involving Aurora in the cross were found to be monosomic and 4 were disomic. All 3 fertile F_2 plants involving Kanota were monosomic. Chromosome pairing in the fertile plants was normal.

Since Johnson (16) found marked correlation between high degree of germinability and sativa type of grain, it appears that the absence of the c-chromosome from the sativa parent is responsible for the great increase in the percentage of dormant F_2 seeds. It is unfortunate that a number of 42-chromosome hybrid seeds were not obtained as that would have given a good indication of the relative importance of the genetic make up of the embryo and the surrounding maternal tissue in inducing dormancy.

Although the F_1 seed germinated upon the first wetting, the presence of 42-chromosome F_1 seed would have indicated whether there is any difference between the 41-and 42-chromosome seeds in rate of germinability. A fairly large number of F_1 seeds would be required for this test.

Since factors have been reported that can induce dormancy in non-dormant seeds (9), the following tests were carried out to check for evidence of a dormancy factor in the hulls of the seed of the F_1 plants.

Twenty seeds of normal Ajax were used in each treatment.

Table 1

Testing hull of F_2 seed for dormancy factor.

Treatment	No. of seeds germinated
Ajax placed in hull of hybrid	16
Check	19
Ajax covered with ground hull of hybrid	19
Check	20

While the difference in germination of the different treatments may not be significant, both treatments involving hull from the hybrids retarded the growth of the seedlings. It appeared that the active factor in the hull may not have penetrated the embryo area rapidly enough to have an effect on germination. Another possibility was that the concentration of the active factor was too low to inhibit germination.

In order to increase the possible effect of the hybrid hull extract on germination, only the embryos of normal Ajax were used in the following test.

Table 2

Testing hull of F_2 seed for dormancy factor using embryo culture

Medium	Water extract of Ajax hulls	Water extract of hybrid hulls
Mineral medium	Growth (Fig. A-1)	Germination only (Fig. B-1)
Mineral medium plus starch	Growth (fig. A-2)	Germination only (fig. B-2)
Orchid agar	Growth (fig. A-3)	Growth (fig. B-3)

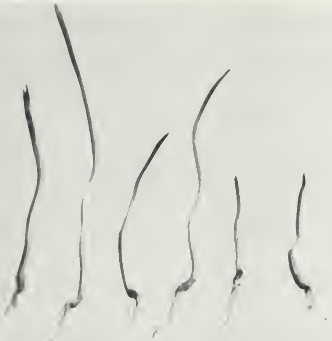

Fig. A-1

Fig. B-1

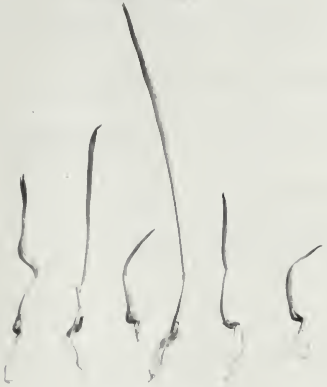

Fig. A-2

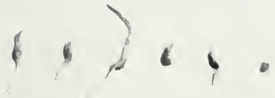

Fig. B-2

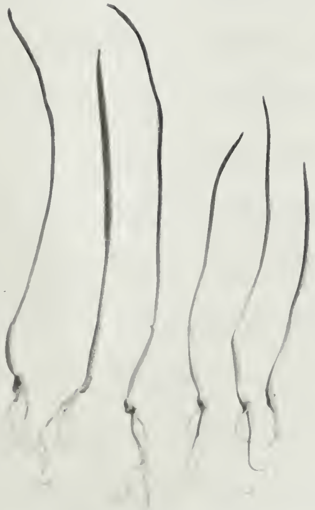

Fig. A-3

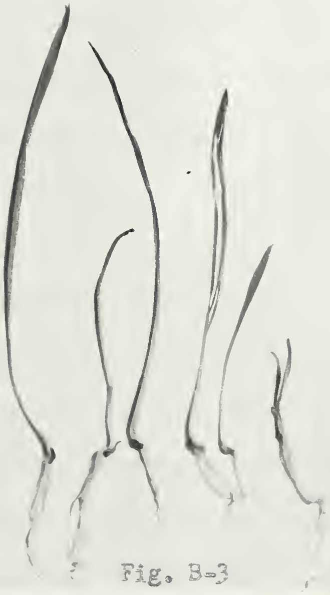

Fig. B-3

Twenty-four hours following the placement of the soaked Ajax embryos on culture medium uniform germination occurred in all treatments. However, by the end of the second day there was definite evidence of a slowing down process in treatments B-1 and B-2.

Embryos in these two treatments did not make any additional growth but remained in an apparently viable state for 8-10 days after which they began to show signs of deterioration.

Although the active factor in the hybrid oat hulls did not prevent germination, it acted as a growth inhibitor. A possible explanation for this is that germination took place as a result of energy obtained from nutrients that were available in the embryo itself prior to the soaking treatment, and the factor that would ordinarily cause dormancy in seeds prevented the synthesis of additional plant nutrients required for further growth. The active factor in the hull could act as an inhibitor of certain metabolic activities.

Reciprocal crosses involving *A. fatua* and monosomic Aurora were repeated in the greenhouse with considerable success. Where *A. fatua* and monosomic Aurora were used as the female parent 44 and 216 F_1 seeds were obtained respectively.

Sixty-five days following pollination the F_1 seeds were subjected to a germination test. Results of plants where 6 or more F_1 seeds were obtained are given in Table 3. Check material of *A. fatua* was obtained by collecting selfed seed from the plant involved in the cross. These seeds came from florets that reached or/were just past anthesis during the time that the crosses were made. Where less than

Table 3

Germination test on F_1 seed from reciprocal crosses involving A. fatua and A. sativa.

Plant no.	Cross	No. of Seeds	Days to Germination 5	6	7	8	9	10	11	12	13	14	15	Percent Germination
1.	A. fatua x Aurora	10		5	2	3								100%
	A. fatua (check)	12					1		3					33%
2.	A. fatua x Aurora	9				5	3		1					100%
	A. fatua (check)	12												0
3.	A. fatua x Aurora	6					1		1	2		2		100%
	A. fatua (check)	12												0
4.	Aurora x A. fatua	7	3	2		2								100%
	Aurora (check)	12	2	10										100%
5.	Aurora x A. fatua	8	4	2	2									100%
6.	Aurora x A, fatua	9				3	4		2					100%
7.	Aurora x A. fatua	6	2	2	2									100%
8.	Aurora x A. fatua	12	9	3										100%
9.	Aurora x A. fatua	19	12	7										100%
10.	Aurora x A. fatua	14	12	2										100%
11.	Aurora a A. fatua	9	3	6										100%

6 F_1 seeds were obtained per plant, the seeds were germinated without a'check' test, however, the results were comparable to those given in Table 3.

Results in Table 3 indicate that delayed germination is genetically recessive to the germinative capacity of the sativa parent. There is a very strong indication that the maternal tissue surrounding the embryo is a factor in delaying germination. The F_1 seeds from the crosses where Aurora was the female parent germinated much more readily than the reciprocal cross.

A check was made as to whether disomic F_1 germinated more readily than monosomic, however, there was no evidence to support this idea since seeds from most plants germinated over a fairly short interval. The germination test should be run as soon as possible after the seeds have matured. Monosomics germinated just as readily as disomics but were not quite as vigorous.

A further germination test on F_2 seed from monosomic F_1 plants as compared to disomic F_1 plants would be of interest.

CONCLUSION

Interspecific crosses between the tetraploid (wild type articulation) and the hexaploid species (sativa type articulation) indicated dominance of the articulation type of the hexaploid parent. Utilizing lines of the above two species, both of which are monosomic for a c-chromosome, resulted in 33- and 34-chromosome F_1 plants. In the 34-chromosome F_1 plant where the c-chromosome of the sativa parent was absent and in the 33-chromosome F_1 plant where the c-chromosome of both parents is absent, the florets developed the fatuoid complex, which consists of an oval or wild disarticulating surface surrounded with dense pubescence, a pubescent rachilla and a geniculate awn on each grain.

Since the pubescence of the lemmas on the 34-chromosome F_1 plants is not as heavy as on the original 28-chromosome parent and the lemmas of the 33-chromosome F_1 plant are glabrous, it is concluded that the factor for pubescence of lemmas is located on this chromosome in the tetraploid parent.

Chromosome pairing in the interspecific hybrids indicated that these two species had one genome in common. The difference in the average number of bivalents in the 34- and 35-chromosome F_1 plants indicates that the c-chromosome is one of the homologous group.

Crosses involving lines of _Avena sativa_ that were monosomic for a c-chromosome and _Avena fatua_ resulted in monosomic F_1 plants which showed a fatuoid complex. In the F_2, plants that were nullisomic for the c-chromosome pair also expressed the fatuoid complex. However, the

florets were sterile. Apparently there is a gene or genes on the c-chromosome that controls normal chromosome pairing. Cytological analysis indicated a high degree of asynapsis in the P.M.C.'s of nullisomic plants. It was also noticed that the factor for pubescence of the lemmas in the *Avena fatua* is also present on the c-chromosome. Pubescence on the lemmas of *A. fatua* is denser than on the monosomic F_1 while the lemmas of nullisomics are glabrous.

A large number of reciprocal crosses were made involving *Avena sativa* and *A. fatua* in order to check for possible linkage between the fatuoid complex and delayed germination. However, the monosomic F_1 plants germinated as readily as the disomic F_1 plants, thus giving no evidence to support this idea.

SUMMARY

1. The heterozygous monosomic fatuoid in Aurora and the 27-chromosome plant were obtained from I. Nishiyama.

2. A heterozygous monosomic fatuoid was discovered in the variety Kanota. It resembled the fatuoids belonging to the modified B series.

3. Interspecific crosses involving the tetraploid (wild type articulation) and the hexaploid (sativa type articulation) indicated dominance of the sativa type articulation. Awns were present on the primary kernel only.

4. Absence of both c-chromosomes, or presence of one or two c-chromosomes that do not suppress awning, results in awns on each floret of the spikelet. Presence of one c-chromosome that suppresses awning results in development of awns on the primary kernel only.

5. Utilizing lines of the above tetraploid and hexaploid species that were monosomic for the c-chromosomes indicated that, in the absence of the c-chromosome of the sativa parent, the florets of both 33-and 34-chromosome F_1 had developed the fatuoid complex. The 33-chromosome plant is a double monosomic, lacking a c-chromosome from both parents.

6. Pubescence on the lemmas of both primary and secondary florets was found to be associated with the c-chromosome pair in the above tetraploid and hexaploid species. Density of the pubescence depends on whether one or two of the c-chromosome carrying that factor are present. Absence of both c-chromosomes results in glabrous lemmas.

7. Crosses involving monosomic Aurora and other hexaploid varieties as well as A. fatua indicated that there is a gene or genes linked with the fatuoid character that affects normal chromosome pairing during meiosis. Absence of both c-chromosomes in all these plants resulted in extremely low bivalent formation and high sterility.

8. Reciprocal crosses involving A. fatua and monosomic sativa indicated that delayed germination is recessive to the germinative capacity of the sativa parent.

9. In reciprocal crosses where A. fatua was used as the female parent, the F_1 seeds did not germinate as readily as the reciprocal cross, thus indicating the importance of the maternal tissue surrounding the embryo.

10. No evidence was obtained in support of a factor for dormancy being linked with the fatuoid complex as the monosomic F_1 seeds germinated as readily as the disomic F_1.

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